Distribution, Morphometry, and Seasonal Biology of the Planktonic Copepods, *Calanus tenuicornis* and *C. lighti,* in the Pacific Ocean[1]

MICHAEL M. MULLIN[2]

THE ECOLOGY of sympatric, congeneric species has been extensively studied on the supposition that such species require rather similar resources and are therefore potential competitors when they co-occur. The pelagic environment is of great areal extent, low faunal diversity, and high physical homogeneity in comparison with terrestrial environments, and hence the nature of the niches of closely related, oceanic species of zooplankton is of some interest (Mullin, 1967). The present investigation concerns the geographical and vertical distribution of two such species, the question of character displacement in size of body and mouthparts, and the extent to which the two species have different breeding seasons.

Bowman (1955) established *Calanus lighti* as a new species, distinguishing it from *Calanus tenuicornis* Dana in collections from the eastern North Pacific by the former's greater length, relative slenderness, and possession of a dorsal elevation or hump at the posterior border of the head. The morphology of the mouthparts, swimming legs, and female genital segments is quite similar in the two species, and they have been referred to as siblings (Mayr, 1963:47) because of their morphological similarity, overlapping distributions, and presumed reproductive isolation. Bowman found no specimens which were intermediate in bodily form, and noted that *C. tenuicornis* was the more widely distributed in the Pacific. Both species were retained in the genus *Calanus* s. str. because they lack a strong, hooked spine on the anterior surface of the second basipodal segment of the first pair of swimming legs; this spine is characteristic of the two other *Calanus* (s. l.) with elongate first antennae, *Neocalanus* (*Calanus*) *gracilis* and *N. robustior,* which often occur in the same samples (see also Brodsky, 1967). In the two species of *Neocalanus*, the urosome is thicker, relative to its length, and the caudal furcae shorter, relative to width, than in *Calanus tenuicornis* and *C. lighti.*

I have found Bowman's descriptions to be adequate in making a clear distinction between the two species in most of the Pacific. The difference in size and the presence of the dorsal hump in *C. lighti* can be detected at least as early as copepodite stage IV. The ratio of mandibular width to prosomal length (see below) also separates the two species. I found no intermediate forms occurring sympatrically with the "pure" forms, supporting Bowman's findings, but a form intermediate in some respects occurred allopatrically south of 40°S (Fig. 1). This form is discussed below as the "Intermediate Form," while the names *C. tenuicornis* and *C. lighti* are reserved for populations clearly distinguishable by all criteria. Since *C. tenuicornis* is reported from 52°S in the western Pacific (Farran, 1929, cited in Vervoort, 1946: 24), the "Intermediate Form" should probably be referred to *C. tenuicornis* until its taxonomic status is clearly established.

DISTRIBUTION OF *C. tenuicornis* AND *C. lighti* IN THE PACIFIC

Plankton collections at Scripps Institution of Oceanography were examined for presence of the copepodite stage V's and adults of the two species. The samples examined were from the following expeditions: Shellback 1952, Capricorn 1952–53, Transpac 1953, Norpac 1955

1 Manuscript received April 23, 1969.

2 Institute of Marine Resources, University of California at San Diego, La Jolla, California 92037.

(samples examined by Gerald Johnson, Arthur Barnett, and Jed Hirota), Troll 1955, Equapac 1956, Downwind 1957–58, Step I 1960, Tethys 1960, Monsoon 1960–61, and Scorpio 1967. Information on these expeditions may be found in Snyder and Fleminger (1965). The samples were from oblique tows made to various depths in the upper 400 meters of water, generally with a net of 1 meter mouth diameter and 500–550μ mesh netting. Because the tows were taken in a variety of ways, often to a depth insufficient to sample the entire population, and because the nets were probably too coarse to retain the smaller copepods quantitatively, only presence or absence and relative abundances of the two species in single tows were recorded, and no contours were drawn.

Calanus tenuicornis ranges from within the Transition Zone of the North Pacific through the Central Water of the South Pacific (Fig. 1), and is thus a warm-water cosmopolite (terminology from McGowan, 1969). *C. lighti* inhabits the Central Water of both hemispheres, but may be divided into two distinct populations by the equatorial current system. If the two populations of *C. lighti* are continuous in dis-

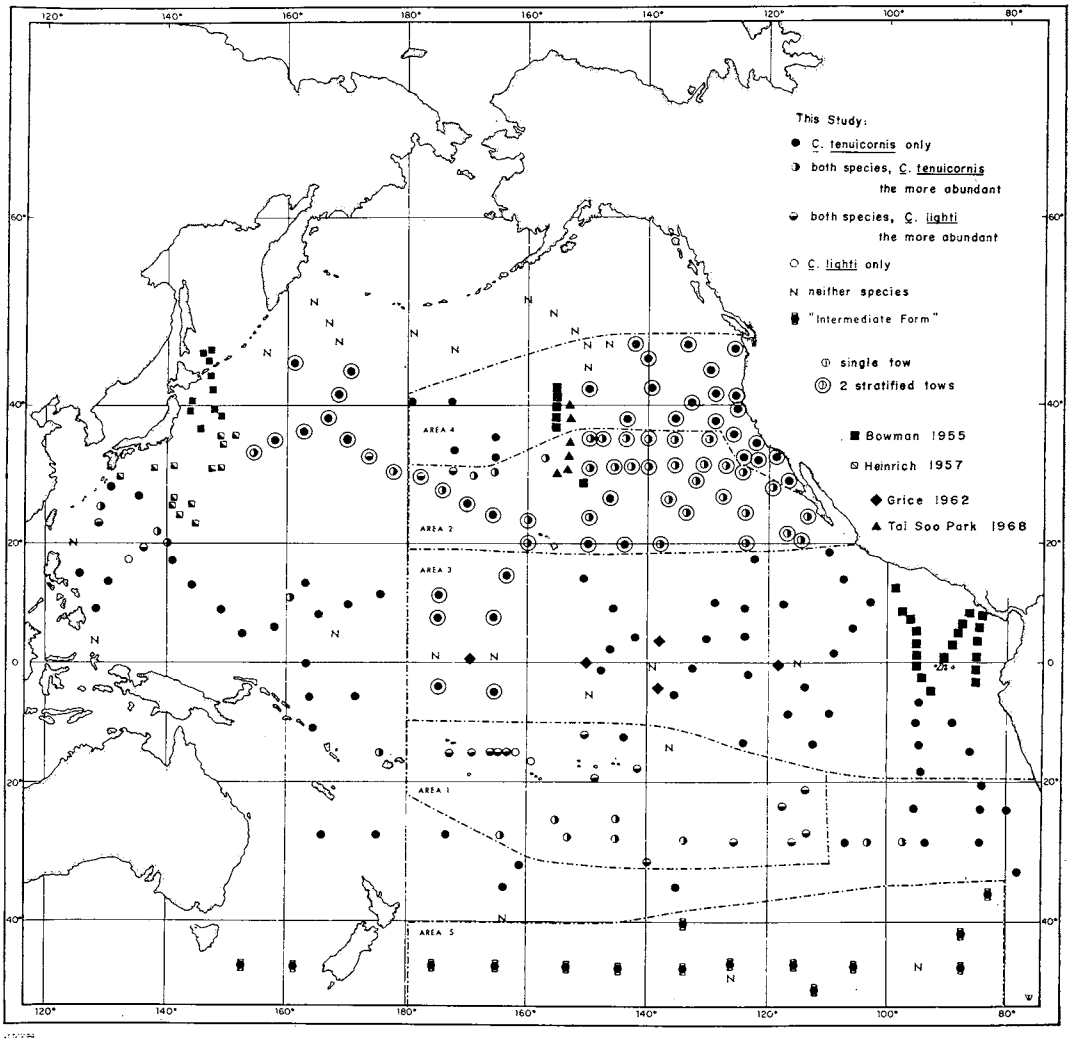

FIG. 1. Distribution of *Calanus tenuicornis* and *C. lighti* in the Pacific Ocean. A circled symbol indicates that two stratified tows were made at that station.

tribution, the connection between them is on the western side of the Pacific.

No *C. lighti* were found in samples from the following locations in the Indian Ocean: 13°S, 110°E; 17°S, 93°E; 13°S, 75°E; 20°S, 58°E; 24°S, 74°E; and 28°S, 74°E. Each of these samples contained *C. tenuicornis*. It is unlikely that *C. lighti* occurs in the Indian Ocean.

Although there are large areas where *C. tenuicornis* is allopatric (the term is used in the sense of Kohn and Orians, 1962:121, to refer to those populations of a species which occur in areas where some other particular species is absent, as distinct from sympatric populations which inhabit areas where the ranges of the two species overlap), there are no large, allopatric populations of *C. lighti*. *C. lighti* tends to be more abundant than its congener in the South Pacific Central Water, but the reverse is true of the North Pacific Central Water.

Stratified tows which divided the water column into approximately 0–150-meter and 150–300-meter intervals were made at Transpac, Norpac, and Equapac stations (Fig. 1). Heinrich (1957) reported that both species of *Calanus* occurred at least to a depth of 500 meters off Japan, but I found *C. lighti* below 150 meters in only one of 33 possible cases. *C. tenuicornis* generally occurred in both depth intervals if it occurred in either, but was usually more abundant in the shallower of the two tows (significance by sign test), especially at night.

Stratified samples were taken from seven depth intervals with Bongo nets (McGowan and Brown, 1966) on a transect along 155°W longitude during two cruises, Ursa Major and Zetes. The copepodite stage V and adult *C. lighti* were found only in the upper 100 meters during both cruises (Fig. 2). *C. tenuicornis* occurred almost exclusively below 50 meters in September, but its range extended to the surface in January. Temperature was not the sole cause of the vertical distribution of either species; each was found in colder water in the northern part of its range than in the southern part of the transect.

In September, at least part of the *C lighti* population lived at shallower depths than did any mature *C. tenuicornis*, which might reduce interspecific competition. During January, however, the vertical range of *C. lighti* was completely included within the range of its more abundant congener.

SIZE OF BODY AND MOUTHPARTS OF *C. tenuicornis* AND *C. lighti*

If differences in body size indicate or make possible differences in selectivity of filter feeding between congeneric species (Hutchinson, 1951), then size might show character displacement (Brown and Wilson, 1956). Thus one would expect that the difference in mean body size between *Calanus lighti* and *C. tenuicornis* would be greater and the variability around each mean smaller in sympatric populations than in allopatric ones. However, body size is affected by temperature and by the availability of food during growth (Deevey, 1960, 1964), and character displacement of body size could occur without regard to selective feeding if size is important in specific recognition and hence in reproductive isolation (see Fleminger, 1967; Frost and Fleminger, 1968).

Size of mouthparts might bear a more direct relationship to preference for food, larger mouthparts being necessary to feed on larger particles. The effects of temperature and supply of food on size can be removed by examining the ratio of mouthpart size to body size. One would expect that, if character displacement has occurred, the ratio of mouthpart size to body size would be smaller in *C. tenuicornis*, the smaller of the two species, than in *C. lighti* —at least where the two species are sympatric. If *C. lighti*, because it is larger, is better able to graze large particles, and *C. tenuicornis* small ones, then character displacement of size of mouthparts should increase this distinction.

I found previously (Mullin, 1963) for *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* in the Gulf of Maine that the ratio of mouthpart size to body size decreased with increasing body size if second antennae or maxillipeds were the mouthparts concerned, but that the width of the molariform edge of the mandibular blade (gnathobase) had a constant ratio to body length, so that regression of ratio on length was not necessary to compare animals of different lengths.

The length of the prosome (= cephalothorax) was used as a measure of body size. Up

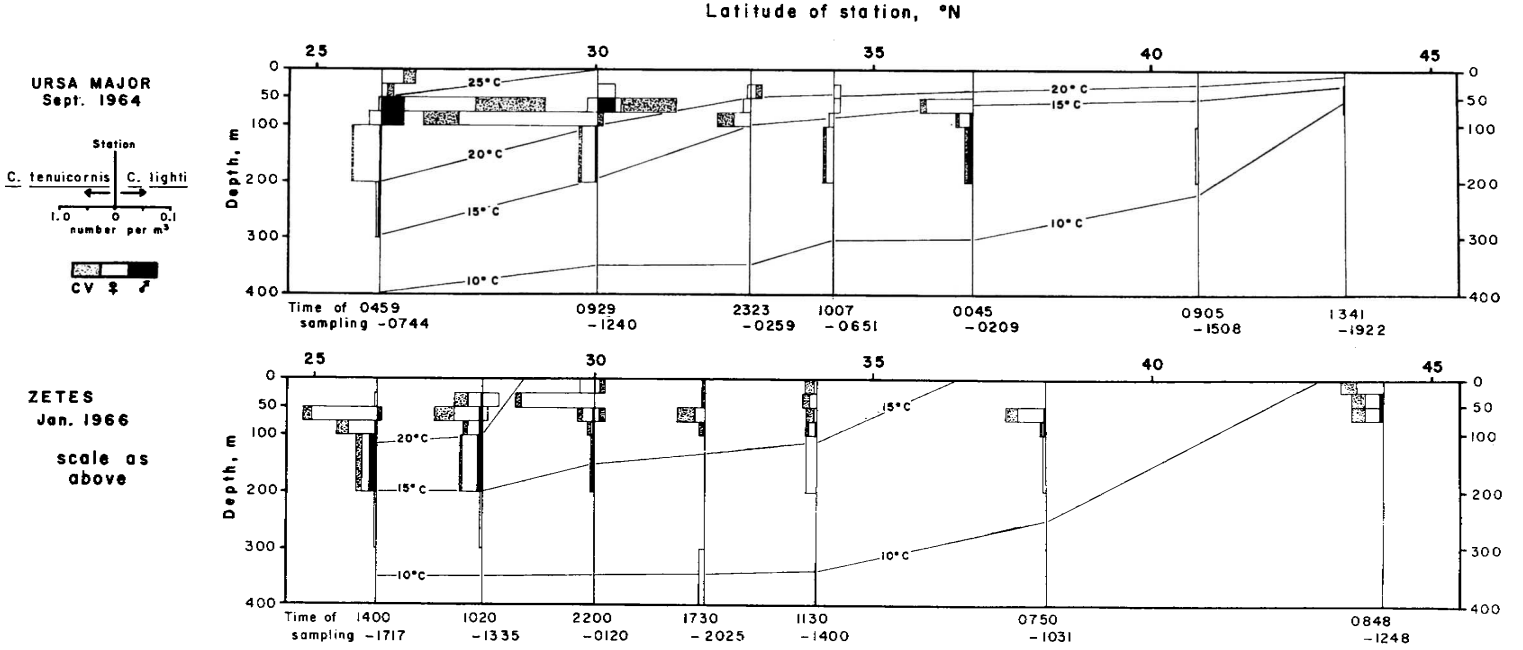

FIG. 2. Vertical distribution of copepodite stage V and adult *Calanus tenuicornis* and *C. lighti* during two transects along 155°W longitude. Samples were taken from the following depth intervals: 0–25 meters, 25–50 meters, 50–75 meters, 75–100 meters, 100–200 meters, 200–300 meters, and 300–400 meters. Note that the scales of abundances for the two species differ. Approximate positions of isotherms are shown.

to 10 animals each of copepodite stage V, females, and males of each species were measured in each sample by means of an ocular micrometer. The mandibles of up to 5 of these animals in each category were dissected off and the width of one molariform edge measured, also by means of an ocular micrometer. Since males have greatly reduced mandibles, as in other species of the genus, the mandibles of only copepodite stage V's and females were examined. The ratio of the width of the prosome, measured from the dorsal aspect halfway along its length, to prosomal length was determined for at least 15 females from each geographic area.

The stations east of 180° from which animals were taken for measurement were grouped into five areas (see Fig. 1). Area 1 samples were from the central South Pacific where *C. lighti* was often more abundant than *C. tenuicornis*. Area 2 samples, in which *C. tenuicornis* was usually the more abundant, were from the central North Pacific. *C. tenuicornis* occurred allopatrically in Area 3, the equatorial Pacific, and in Area 4, the North Pacific Transition Zone and northern California Current.

The measurements summarized in Table 1 showed that both species were significantly smaller ($p < 0.005$ by t test in all cases) and less variable ($p < 0.01$ by ratio of variances in all cases) in Area 1 than in the other areas. There was no overlap in size of a particular developmental stage between the species in one area, confirming Bowman's (1955:418) findings, although the smallest *C. lighti* in Area 1 were the same size as the largest *C. tenuicornis* from the other areas. The difference in size between *C. tenuicornis* copepodite stage V's from Area 2 and those from Area 3 was significant ($p < 0.05$), but neither the males nor

TABLE 1

LENGTH OF PROSOME (= CEPHALOTHORAX), RATIO OF PROSOMAL WIDTH TO LENGTH, AND RATIO OF MANDIBULAR WIDTH TO PROSOMAL LENGTH OF *Calanus lighti* AND *C. tenuicornis**

		Calanus lighti			*Calanus tenuicornis*		
		FEMALE	MALE	COPEPODITE V	FEMALE	MALE	COPEPODITE V
		Prosomal Length (millimeters)					
Area 1	$\bar{x}$	1.83	1.58	1.48	1.37	—	1.16
	95% c.l.	±0.11	±0.08	±0.10	±0.13	—	±0.08
	n	160	72	104	104	—	14
Area 2	$\bar{x}$	2.04	1.81	1.66	1.48	1.35	1.26
	95% c.l.	±0.22	±0.12	±0.18	±0.21	±0.18	±0.16
	n	124	27	100	373	88	240
Area 3	$\bar{x}$	—	—	—	1.49	1.34	1.23
	95% c.l.	—	—	—	±0.20	±0.14	±0.18
	n	—	—	—	266	37	122
Area 4	$\bar{x}$	—	—	—	1.60	1.44	1.33
	95% c.l.	—	—	—	±0.20	±0.14	±0.13
	n	—	—	—	182	52	127
		Prosomal width/length					
Area 1	$\bar{x}$	0.27	—	—	0.30	—	—
Area 2	$\bar{x}$	0.28	—	—	0.31	—	—
Area 3	$\bar{x}$	—	—	—	0.32	—	—
Area 4	$\bar{x}$	—	—	—	0.31	—	—
		Mandibular width/prosomal length					
Area 1	$\bar{x}$	0.063	—	0.063	0.074	—	0.074
Area 2	$\bar{x}$	0.064	—	0.062	0.075	—	0.074
Area 3	$\bar{x}$	—	—	—	0.076	—	0.073
Area 4	$\bar{x}$	—	—	—	0.075	—	0.073

* The mean ($\bar{x}$), number of individuals measured (n), and 95% confidence limits (95% c.l.) are given for prosomal length in each of the four areas shown in Figure 1.

the females were significantly different between these two areas. *C. tenuicornis* individuals from Area 4 were significantly larger in all stages than those from other areas. The variability in size was no greater in Area 3 or Area 4 than in Area 2, suggesting that the absence of the presumed competitor, *C. lighti*, has not broadened the niche of *C. tenuicornis* as reflected in body size.

Table 1 also confirms Bowman's observation that *C. lighti* is more slender relative to its length than *C. tenuicornis*. The differences between the species in Areas 1 and 2 are significant ($p < 0.01$) by rank sum test.

Mandibular width was in relatively constant ratio to prosomal length within each species, but there was no evidence for character displacement of mouthpart size (Table 1). The smaller species had the larger mandible/prosome ratio, so the mandibles of the two species are more similar in size than are the bodies. Further, the mandible/prosome ratio was not significantly different in *C. tenuicornis* from Areas 1 and 2, where it is sympatric with *C. lighti*, than that in Areas 3 and 4, where it is allopatric.

Hutchinson (1959:152) concluded from measurements on mammals and birds that, where congeneric species coexist, the ratio of the size of a particular food-gathering structure of the larger species to the size of that structure in the smaller species should be about 1.3 to allow separation of trophic niches. The ratios of prosomal lengths in sympatric populations of *C. lighti* and *C. tenuicornis* are slightly greater than this (range 1.28–1.38), but the ratios of mandibular widths are much less (range 1.09–1.18). *C. lighti* and *C. tenuicornis* do not, therefore, show the degree of morphometric difference in trophic structure which one might expect from sympatric congeners. The results support the conclusions of Fleminger (1967) for *Labidocera* and Frost and Fleminger (1968) for *Clausocalanus* that character displacement in trophic structures of congeneric, planktonic copepods is much less common than displacement of reproductive characters.

MORPHOMETRY OF THE INTERMEDIATE FORM

The Intermediate Form might be designated *Calanus lighti* except that it lacks the dorsal hump, has the opaque appearance more characteristic of *C. tenuicornis* than *C. lighti*, and is distributed symmetrically with the North Pacific Transition Zone population of *C. tenuicornis*. The appendages are very similar to those of both *C. tenuicornis* and *C. lighti*. A comparison of Table 2 with Table 1 shows that the Intermediate Form is morphometrically more like *C. lighti* than *C. tenuicornis*. However, the male is larger relative to the female than is the case in either *C. lighti* or *C. tenuicornis*.

TABLE 2
LENGTH OF PROSOME, RATIO OF PROSOMAL WIDTH TO LENGTH, AND RATIO OF MANDIBULAR WIDTH TO PROSOMAL LENGTH OF THE "INTERMEDIATE FORM" FROM AREA 5 IN FIGURE 1 (COMPARE WITH TABLE 1)

	FEMALE	MALE	COPEPODITE V
	Prosomal Length (mm)		
$\bar{x}$	1.85	1.75	1.50
95% c.l.	±0.16	±0.16	±0.16
n	70	20	45
	Prosomal Width/Length		
$\bar{x}$	0.28	—	—
	Mandibular Width/Prosomal Length		
$\bar{x}$	0.065	—	0.065

The Intermediate Form is certainly not a hybrid since the parental, "pure" forms are absent in the area in which it occurs. If it is simply an ecophenotype of *C. tenuicornis*, it is surprising that trends toward slenderness and reduction in relative size of the mandible are not shown in the North Pacific Transition Zone population of this species. It would be more correct to consider the population of the Intermediate Form a geographic isolate of *C. tenuicornis*, differing genetically from the populations further north. If this interpretation is correct, the Intermediate Form shows morphometric convergence toward the phenotype of *C. lighti*.

SEASONALITY OF REPRODUCTION

Male *Calanus tenuicornis* and *C. lighti* have greatly reduced mandibular blades (see Fig. 2c of Bowman, 1955) and probably do not survive in the adult stage nearly as long as do the females because of starvation. Hence, if breeding activity is strongly seasonal, the ratio of males

to total adults should be much higher during the breeding season than during the rest of the year. Conversely, the ratio would show rather little variation throughout the year if breeding occurred continuously. A breeding season, when determined by the ratio of the sexes, obviously refers to the period during which there is a high probability that any individual female has recently been impregnated and is ready to begin laying eggs. Females in the genus *Calanus* do not carry the spermatophores for a long enough period to allow one to use their frequency as an index of copulation.

Samples from the eastern central North Pacific (here defined as the area bounded by 20°N, 35°N, 125°W, and 160°W) are available for most months of the year in collections made by the Marine Life Research–California Cooperative Oceanic Fisheries Investigation cruises in the California Current and some of the expeditions cited previously. Adults of both species were counted in aliquots of these samples. The mean ratio of males to total adults for all samples from each half-month period was plotted (Fig. 3) regardless of the year or the particular location from which the samples came. Samples from at least two locations were examined for each half-month period.

This procedure obscures year-to-year or location-to-location variation in the relative abundance of males, and so the correlation coefficient between the sex ratios of the two species was calculated for all samples in which both sexes of both species were found. A positive correlation would suggest that the same conditions favored reproduction by both species, while a negative correlation would suggest separation of reproductive activity in space and/or time.

The samples examined were generally from tows taken in the upper 150 meters of water, a depth of tow which is adequate to sample the entire population of *C. lighti* but not that of *C. tenuicornis*. This in itself would cause no problem since only the ratio of the sexes is of interest, but examination of the stratified tows (Fig. 1) showed that shallow tows are probably strongly biased against the males of *C. tenuicornis* ($p < 0.005$ by sign test that the sex ratio was the same in shallow and deep tows). Information in Figure 2 confirms this finding. Further, male *C. tenuicornis* are the least likely adult form to be retained quantitatively by coarse mesh, since they are the smallest. Therefore the ratios shown in Figure 3 for this species are almost certainly too low, and it can only be assumed that changes in the true sex ratio would be reflected correctly in the samples examined.

Figure 3 suggests that reproductive activity

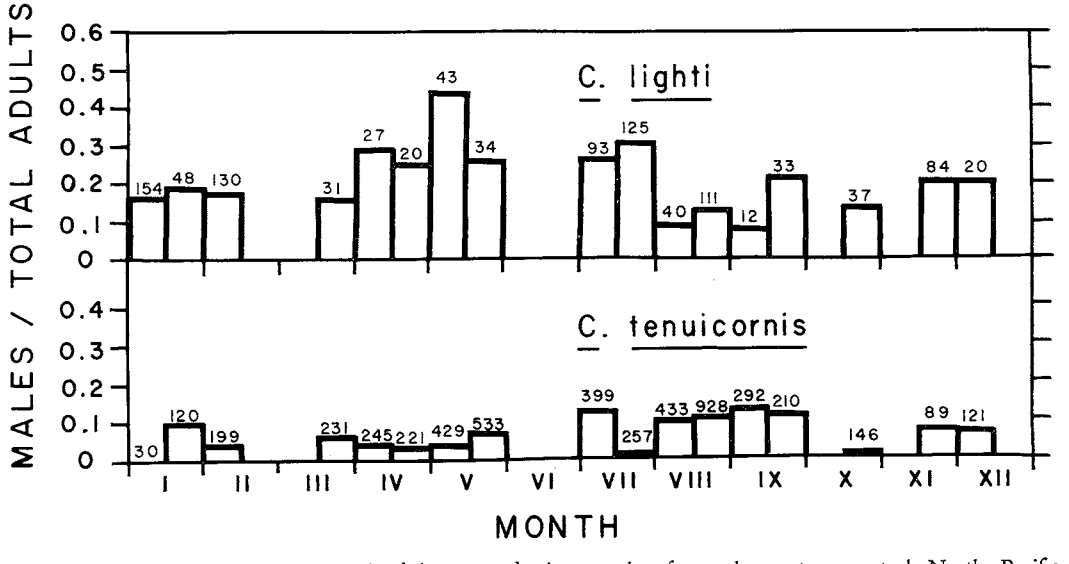

FIG. 3. The ratio of male to total adult copepods in samples from the eastern central North Pacific Ocean. The number above each bar indicates the total number of adults counted.

occurs throughout the year in the population of *C. lighti*, as is the case for other tropical copepods (Heinrich, 1963), the late spring and early summer being the most important period. No major seasonality in breeding could be detected in the population of *C. tenuicornis*, although the results are difficult to evaluate for the reasons mentioned above. Breeding activity may be more intense in late summer and early fall that at other times of year, but the evidence is only suggestive. There was no significant positive or negative correlation between the sex ratios of the two species. Thus, there is no clear evidence for spatial or temporal differences in conditions promoting reproductive activity of the two species in the central North Pacific.

The extent of competition between juvenile stages would be affected not only by differences in the seasons of their occurrence, which examination of the sex ratios of the adults suggests are small, but also by the relative abundance of these stages, which is in turn affected by the relative abundance of the parental adults in various areas during various seasons. The available samples are not adequate to make this estimate, except to note that *C. tenuicornis* is apparently the more abundant species in all seasons in the North Pacific.

DISCUSSION

There is no reason as yet to synonymize *Calanus tenuicornis* and *C. lighti* by considering them to be morphs or subspecies, since they are sympatric and distinct over large areas and since what I have called the Intermediate Form is allopatric from both. Experimental rearing of eggs from females of both morphological types under a variety of conditions, extending the work of Matthews (1966) on *C. finmarchicus* and *C. glacialis*, is desirable.

The two species studied here would seem to be potential competitors in areas of sympatry unless the vertical ranges of the populations remain at least partially separate for most of the year. Of interest would be studies of the vertical distribution of younger stages within these areas, differences in selective feeding (see Fryer, 1954, on fresh water *Diaptomus*) which are not reflected in morphology of the mouthparts, and the possibility of control by different predators (see Brooks and Dodson, 1965; Brooks, 1968, concerning the effects of predation on intergeneric competition in fresh water).

SUMMARY

1. *Calanus lighti* is an epiplanktonic species largely restricted to the Central Water masses of the North Pacific and South Pacific, while *C. tenuicornis* is a warm-water cosmopolite which lives to a depth of at least 200 meters. The adults of the latter species were uncommon in water shallower than 50 meters in September, but extended up to the surface in January. An "Intermediate Form" occupies the Transition Zone of the South Pacific.

2. No evidence for character displacement in size of mouthparts was found.

3. Both species probably breed throughout the year in the eastern central North Pacific, and there is little evidence for separation of reproductive activity within the area of sympatry.

ACKNOWLEDGMENTS

This research was supported in full by the United States Atomic Energy Commission, Contract No. AT(11-1)GEN 10, P.A. 20. Contribution from the Scripps Institution of Oceanography. Dr. Abraham Fleminger gave advice and encouragement during the study and improved the manuscript through his helpful comments.

LITERATURE CITED

BOWMAN, THOMAS E. 1955. A new copepod of the genus *Calanus* from the northeastern Pacific with notes on *Calanus tenuicornis* Dana. Pacific Science, vol. 9, pp. 413–422.

BRODSKY, K. A. 1967. Types of female genitalia and heterogeneity in the genus *Calanus* (Copepoda). (English translation.) Doklady Akad. Nauk S.S.S.R., vol. 176, pp. 222–225.

BROOKS, JOHN L. 1968. The effects of prey size selection by lake planktivores. Systematic Zoology, vol. 17, pp. 273–291.

BROOKS, JOHN L., and S. I. DODSON. 1965. Predation, body size, and composition of plankton. Science, vol. 150, no. 3692, pp. 28–35.

BROWN, WILLIAM L., JR., and E. O. WILSON. 1956. Character displacement. Systematic Zoology, vol. 5, pp. 49–64.

DEEVEY, GEORGIANA B. 1960. Relative effects of temperature and food on seasonal variations in length of marine copepods in some eastern American and western European waters. Bulletin of the Bingham Oceanographic Collection, vol. 17, pp. 54–86.

——— 1964. Annual variations in length of copepods in the Sargasso Sea off Bermuda. Journal of the Marine Biological Association of the United Kingdom, vol. 44, pp. 589–600.

FLEMINGER, ABRAHAM. 1967. Taxonomy, distribution, and polymorphism in the *Labidocera jollae* group with remarks on evolution within the group. Proceedings of the U.S. National Museum, vol. 120, no. 3567, pp. 1–61.

FROST, BRUCE, and A. FLEMINGER. 1968. A revision of the genus *Clausocalanus* (Copepoda: Calanoida) with remarks on distributional patterns in diagnostic characters. Bulletin of the Scripps Institution of Oceanography, vol. 12, pp. 1–235.

FRYER, GEOFFREY. 1954. Contributions to our knowledge of the biology and systematics of the freshwater copepoda. Schweizerische Zeitschrift für Hydrologie, vol. 16, pp. 64–77.

GRICE, GEORGE D. 1962. Calanoid copepods from equatorial waters of the Pacific Ocean. U.S. Fish and Wildlife Service, Fisheries Bulletin, vol. 61, no. 186, pp. 172–246.

HEINRICH, A. K. 1957. Distribution of *Calanus tenuicornis* Dana and *Calanus lighti* Bowman in the North Pacific Ocean. (English translation.) Doklady Akad. Nauk S.S.S.R., Biological Science Section, vol. 116, pp. 691–693.

——— 1963. Age-structure features of copepod populations in tropical regions of the Pacific Ocean. (English abstract.) Okeanologiia, vol. 3, pp. 88–99.

HUTCHINSON, G. EVELYN. 1951. Copepodology for the ornithologist. Ecology, vol. 32, 571–577.

——— 1959. Homage to Santa Rosalia, or, why are there so many kinds of animals. American Naturalist, vol. 93, pp. 145–157.

KOHN, ALAN J., and G. H. ORIANS. 1962. Ecological data in the classification of closely related species. Systematic Zoology, vol. 11, pp. 119–127.

MATTHEWS, J. B. L. 1966. Experimental investigations of the systematic status of *Calanus finmarchicus* and *C. glacialis* (Crustacea: Copepoda), pp. 479–492. In: H. Barnes, ed., Some contemporary studies in marine science. London, Allen and Unwin.

MAYR, ERNST. 1963. Animal species and evolution. Cambridge, Harvard University Press. 797 pp.

MCGOWAN, JOHN A. 1969. Oceanic zoogeography of the Pacific. S.C.O.R. (Cambridge) Symposium Volume, The Micropaleontology of the Oceans, Sec. A. (In press.)

MCGOWAN, JOHN A., and D. M. BROWN. 1966. A new opening-closing paired zooplankton net. Scripps Institution of Oceanography Ref. No. 66-23, 56 pp.

MULLIN, MICHAEL M. 1963. Comparative ecology of the genus *Calanus* in the Gulf of Maine. Unpublished Ph.D. thesis, Harvard University. 97 pp.

——— 1967. On the feeding behavior of planktonic marine copepods and the separation of their ecological niches. Marine Biology Association of India, Symposium on Crustacea, pt. 3, pp. 955–964.

PARK, TAI SOO. 1968. Calanoid copepods from the central North Pacific Ocean. U. S. Fish and Wildlife Service, Fisheries Bulletin, vol. 66, pp. 527–571.

SNYDER, H. GEORGE, and A. FLEMINGER. 1965. A catalogue of zooplankton samples in the marine invertebrate collections of Scripps Institution of Oceanography. S.I.O. Ref. No. 65–14, 140 pp., 48 charts.

VERVOORT, W. 1946. Biological results of the Snellius Expedition. XV. The bathypelagic Copepoda Calanoida of the Snellius Expedition. I. Families Calanidae, Eucalanidae, Paracalanidae, and Pseudocalanidae. Temminckia, vol. 8, pp. 1–181.